Aliso: A Journal of Systematic and Evolutionary Botany

Volume 10 | Issue 3 Article 6

1983

Wood Anatomy of Calycanthaceae

Sherwin Carlquist

ALISO
10(3), 1983, pp. 427–441

WOOD ANATOMY OF CALYCANTHACEAE: ECOLOGICAL AND SYSTEMATIC IMPLICATIONS

Sherwin Carlquist

INTRODUCTION

Wood anatomy of Calycanthaceae has not been studied as a unit. Wood features of the family have been summarized by Metcalfe and Chalk (1950); various authors have mentioned one or more traits in studies dealing with Calycanthaceae (e.g., Wilson 1979) or other families (e.g., Garratt 1934). In view of recent interest in *Idiospermum australiense* (Diels) Blake, a new comparative study is needed. One goal of the present study is clarification of relationships of *Idiospermum* to *Calycanthus* and *Chimonanthus*. Wood anatomy of *Idiospermum* was described by Blake (1972) and Wilson (1979); a new description is offered here to provide more quantitative data. Descriptions of the wood of *Calycanthus* and *Chimonanthus* provided here incorporate such quantitative data, but also modify earlier descriptions with respect to some important qualitative features. Material of the recently described genus *Sinocalycanthus* (Cheng and Chan 1964) was not available, although the description of that genus suggests it is not strongly different from *Calycanthus* or *Chimonanthus*.

The present study incorporates material of *Calycanthus floridus* L. var. *floridus*, *C. floridus* var. *laevigatus* (Willd.) Torr. & Gray, *C. occidentalis* Hook. & Arn., *Chimonanthus praecox* (L.) Link, and *Idiospermum australiense*. Material of *Chimonanthus nitens* Oliver and *C. salicifolia* Hu, the two other species of *Chimonanthus* recognized by Nicely (1965), was not available for study.

The three genera studied here grow in distinctive habitats. *Calycanthus occidentalis* is essentially riparian in distribution and occurs throughout lower montane northern California; *C. floridus* occurs near streams, and on moist slopes, chiefly in understory, in the southeastern United States (Nicely 1965). *Chimonanthus* grows in eastern China, becoming less common to the north and the center, and characterizes cliffs and slopes. *Idiospermum* is found in lowland tropical rain forest areas of northern Queensland (Blake 1972). The question of whether these distinctive habitats are related to wood anatomy of the three genera, respectively, is examined here. In particular, the occurrence of helical thickenings in vessels is of interest with respect to climatic factors.

Calycanthaceae is placed close to Monimiaceae or other families allied to Lauraceae in most systems (e.g., Cronquist 1981; Dahlgren 1980; Thorne

1968, 1983). To which family or families is Calycanthaceae related on the basis of wood anatomy? Data on wood features can contribute to resolution of this question, but only if we understand which characters are related to ecological adaptations and which represent deepseated features which do not seem to be governed by recent evolution into particular habitats.

MATERIALS AND METHODS

Wood samples of *Calycanthus, Chimonanthus,* and *Idiospermum* were available as dried stem portions. The materials are all from cultivation except for the *Idiospermum,* which was collected in the wild. While one can legitimately question variance in quantitative features compared with what one would find in wood of naturally-occurring specimens, the variance is limited in all likelihood, and qualitative features are probably not affected (Stern and Greene 1958). Wood samples were boiled prior to sectioning on a sliding microtome. The wood of *Idiospermum* is very hard, and extended treatment with Kukachka's (1977) ethylenediamine method was therefore required. Sections were stained with safranin. Macerations were prepared with Jeffrey's fluid and stained with safranin. Quantitative features are based on 25 measurements per feature. Specimens documenting this study are cited in the following section; these specimens are located in the herbarium of the Rancho Santa Ana Botanic Garden.

ANATOMICAL DESCRIPTIONS

Calycanthus floridus var. *floridus* (*Carlquist 15666*) (Fig. 3–6). Growth rings present, vessels smaller and more numerous in latewood; growth rings terminate with fibers narrower than those of earlywood. Vessels as seen in transection arranged in very prominent distributions which tend to form diagonal bands. Perforation plates simple. Mean number of vessels per group = 3.5. Mean vessel diameter, 50 μm. Mean vessel-element length, 420 μm. Mean number of vessels per mm^2 transection = 170. Intervascular pitting alternate (Fig. 4), pits circular or polygonal in outline, 9–11 μm in diameter, with small circular to elliptical apertures 1–2 μm in diameter. Vessel-ray pits 7–9 μm in diameter, alternate or opposite with apertures 6–8 μm in diameter. Helical bands and thickenings present in some smaller (latewood) vessels (Fig. 5), not present in most vessels. Tyloses common (Fig. 4, 6), thin walled and spherical in shape. Imperforate tracheary elements all fiber-tracheids, their pits very small (ca. 2 μm in diameter), the borders exceeded a little by the slitlike apertures. Mean fiber-tracheid length, 780 μm. Mean fiber-tracheid diameter, 23 μm. Fiber-tracheid wall thickness, 1.5 μm. Axial parenchyma vasicentric scanty plus marginal (scattered cells which may be termed diffuse both in last-formed latewood and first-formed earlywood). Rays mostly uniseriate, a few biseriate rays present (Fig. 3). Mean

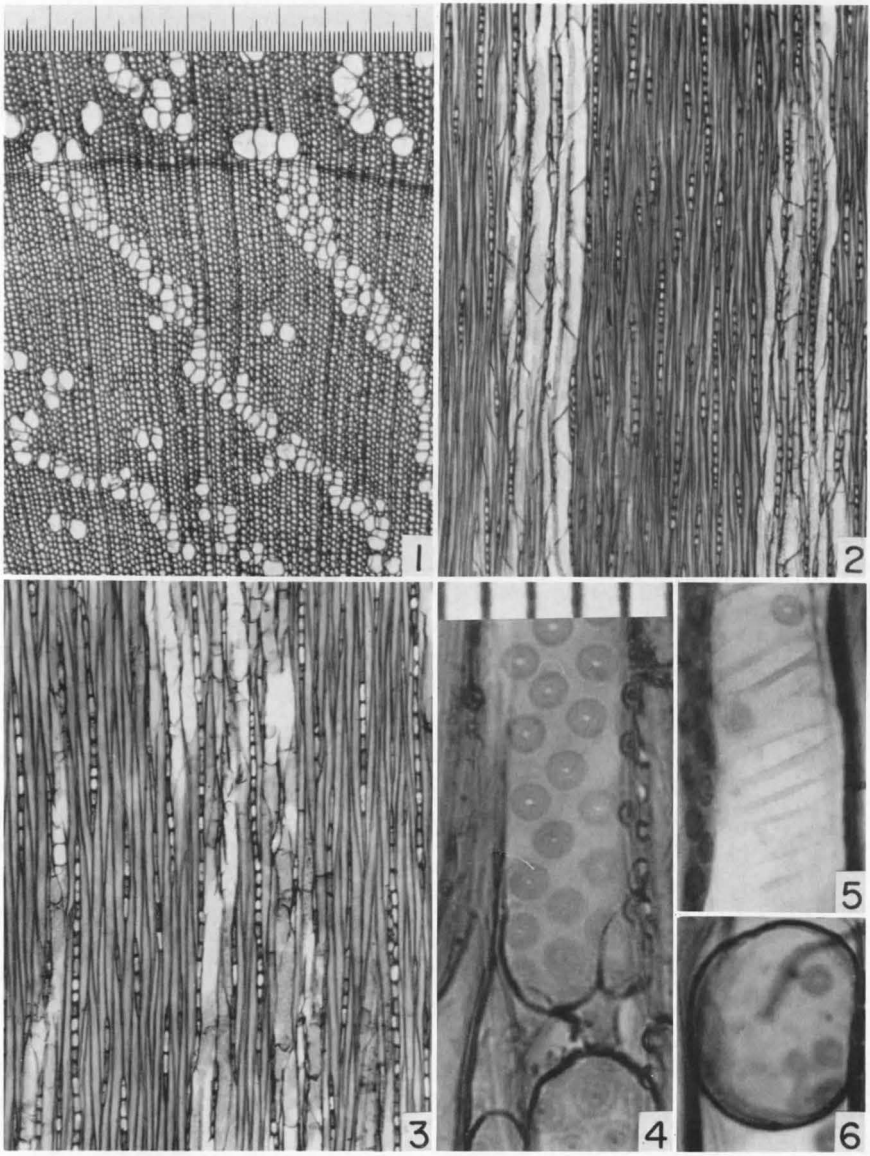

Fig. 1–6. Wood sections of *Calycanthus floridus*.—1–2. *C. floridus* var. *laevigatus* (*Carlquist 15694*).—1. Transection, showing end of growth ring (above) and diagonal bands of vessels.—2. Tangential section; two vessel groupings evident.—3–6. *C. floridus* var. *floridus* (*Carlquist 15666*).—3. Tangential section. Rays taller and with larger cells than in *C. floridus* var. *laevigatus*.—4–6. Portions of vessels from radial sections.—4. Circular pits on vessel walls (portions of tyloses below).—5. Streaklike helical thickenings on vessel wall.—6. Tylosis. (Fig. 1–3, magnification scale above Fig. 1 [finest division = 10 μm]; Fig. 4–6, scale above Fig. 4 [divisions = 10 μm].)

height uniseriate rays, 440 μm. Shorter uniseriate rays composed mostly of erect cells; taller uniseriate rays (as well as biseriate rays) tend to have both procumbent and erect cells. Ray cells with moderately thick walls, some nearly sclereidlike. Some pits on ray cells with borders (pits seen in sectional view in radial sections). Wood nonstoried.

Calycanthus floridus var. *laevigatus* (*Carlquist 15694*) (Fig. 1–2). Growth rings present, vessels smaller and more numerous in latewood (Fig. 1); growth rings terminate with narrower fibers. Vessels as seen in transection arranged in very large distributions which tend to form diagonal bands (Fig. 1). Perforation plates simple. Mean vessel diameter, 38 μm. Mean vessel wall thickness, 1.7 μm. Mean vessel-element length, 304 μm. Mean number of vessels per mm^2 = 231. Intervascular pits alternate, circular or (where crowded) polygonal in outline, 7–9 μm in diameter, with circular or elliptical apertures 1–2 μm in diameter. Vessel-ray pits alternate or opposite, 7–11 μm in diameter, with apertures nearly as wide as the pit cavities. Vessel-axial parenchyma pits 5–7 μm in diameter, otherwise like vessel-ray pits. Helical bands and thickenings present in some narrower (latewood) vessels, not present in most vessels. Imperforate tracheary elements all fiber-tracheids, with small bordered pits about 2 μm in diameter, the slitlike aperture exceeding the border. Mean fiber-tracheid length, 480 μm. Mean fiber-tracheid diameter, 10 μm (latewood) to 26 μm (earlywood). Fiber-tracheid wall thickness, 4.6 μm. Axial parenchyma consists of vasicentric scanty cells plus initial (scattered cells in earliest-formed earlywood, therefore a kind of limited diffuse distribution). Axial parenchyma strands typically of five cells. Uniseriate rays more common than multiseriate rays (Fig. 2), the latter 2–3 cells wide at most. Mean height of uniseriate rays, 279 μm. Mean height of multiseriate rays, 354 μm. Ray cells erect, square, and procumbent; upright cells most common in short uniseriate rays and in tips of long uniseriate rays and in wings of multiseriate rays. Erect ray cells more abundant than procumbent cells in the specimen studied. Ray cells moderately thick walled; many bordered pits seen in sectional view on walls of ray cells in radial sections. Resinlike deposits observed in some ray cells. Wood nonstoried.

Calycanthus occidentalis (*Carlquist 7391*) (Fig. 7–10). Growth rings present (Fig. 7), consisting of narrower vessels and narrower fiber-tracheids in latewood than in earlywood. Vessels distributed in diagonal bands or other pore multiple arrangements (Fig. 7). A few vessels solitary, some vessels in large groups. Mean number of vessels per group = 5.9. Perforation plates simple. Mean diameter of vessels, 58 μm. Mean vessel-element length, 360 μm. Mean number of vessels per mm^2 = 160. Intervascular pits alternate, circular or polygonal in outline, 8–11 μm in diameter, apertures small (2–3 μm in diameter), circular or elliptical in outline. Vessel-ray pitting alternate or opposite circular, with large apertures (ca. 8 μm) as compared to pit-cavity diameter (ca. 10 μm). Helical thickenings present in some narrower

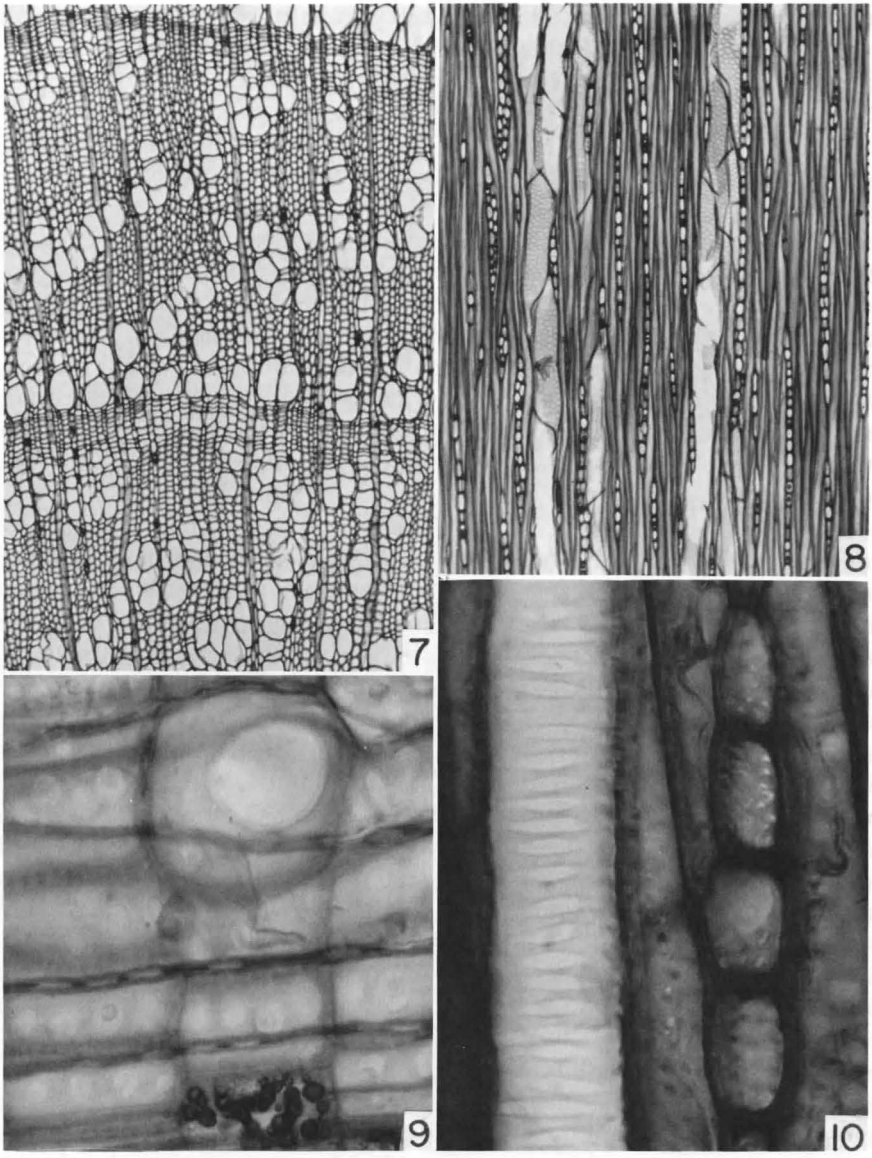

Fig. 7–10. Wood sections of *Calycanthus occidentalis* (*Carlquist 7391*).—7. Transection; end of growth ring, center.—8. Tangential section; earlywood vessels seen in longisection.—9. Radial section, perforated ray cell above; scalariform pitting on vessel-ray contacts, below.—10. Tangential section, illustrating streaklike thickenings on vessel wall, left. (Fig. 7–8, magnification scale above Fig. 1; Fig. 9–10, scale above Fig. 4.)

(latewood) vessels (Fig. 10); thickenings absent in most vessels. Imperforate tracheary elements are all fiber-tracheids with small pits (about 2–3 μm in diameter), the slitlike pit apertures exceeding the diameter of the pit border. Mean fiber-tracheid length, 640 μm. Mean fiber-tracheid diameter, 18 μm. Mean fiber-tracheid wall thickness, 2.7 μm. Axial parenchyma in strands of 2–5 (mostly 4) cells. Axial parenchyma cells vasicentric scanty plus a few scattered (diffuse) at the juncture between earlywood and latewood. Uniseriate rays more common than multiseriate rays; the latter three cells wide at most (Fig. 8). Mean uniseriate ray height, 250 μm. Mean multiseriate ray height, 452 μm. Rays composed of erect, square, and procumbent cells. Erect cells seen more commonly in short uniseriate rays and in wing portions of multiseriate rays. Procumbent ray cells more common in central portions of multiseriate rays. Perforate ray cells occasional (Fig. 9). Ray cells with moderately thick walls; some bordered pits observed in sectional view in radial sections. Some resinlike deposits observed in ray cells (Fig. 9). Wood nonstoried.

Chimonanthus praecox (*Carlquist 1550*) (Fig. 11–15). Growth rings present, vessels smaller and more numerous in latewood, fiber-tracheids narrower and much more thick walled in latewood (Fig. 11). Vessels distributed in extensive bands which take diagonal or chevronlike conformations as seen in transection (Fig. 11). Perforation plates simple. Mean vessel diameter, 67 μm. Mean vessel wall thickness, 2.4 μm. Mean vessel-element length, 270 μm. Mean number of vessels per mm^2 of transection = 201. Some vascular tracheids present in latewood. Intervascular pits circular to elliptical in outline, 6–8 μm in diameter, apertures elliptical in outline (Fig. 15). Vessel-ray pits opposite to alternate, some radially widened, 8–12 μm in diameter, pit apertures large, 7–11 μm in diameter. Helical thickenings present on walls of all vessels (Fig. 14, 15), more pronounced than those of *Calycanthus* latewood vessels. Imperforate tracheary elements all fiber-tracheids, with vestigial borders and slitlike apertures. Mean fiber-tracheid length, 632 μm. Mean fiber-tracheid diameter, 15 μm. Fiber-tracheid wall thickness ranging from 1.2 μm in earlywood to 4.5 μm in latewood. Axial parenchyma vasicentric scanty plus a scattering of cells at margin between latewood and earlywood (in which region the axial parenchyma is therefore distributed in a diffuse fashion). Axial parenchyma strands of 4–5 cells. Rays uniseriate and multiseriate, the multiseriate rays more common. Multiseriate rays essentially all biseriate and triseriate (Fig. 12). Mean uniseriate ray height, 150 μm. Mean multiseriate ray height, 430 μm. Ray cells erect, square, and procumbent. Uniseriate rays and wings of multiseriate rays composed of erect cells; procumbent cells mostly in multiseriate portions of multiseriate rays (Fig. 15). Ray cells relatively thin walled (Fig. 13). Perforated ray cells occasional (Fig. 13). Some pits of ray cells bordered as seen in sectional view on radial sections. Wood nonstoried.

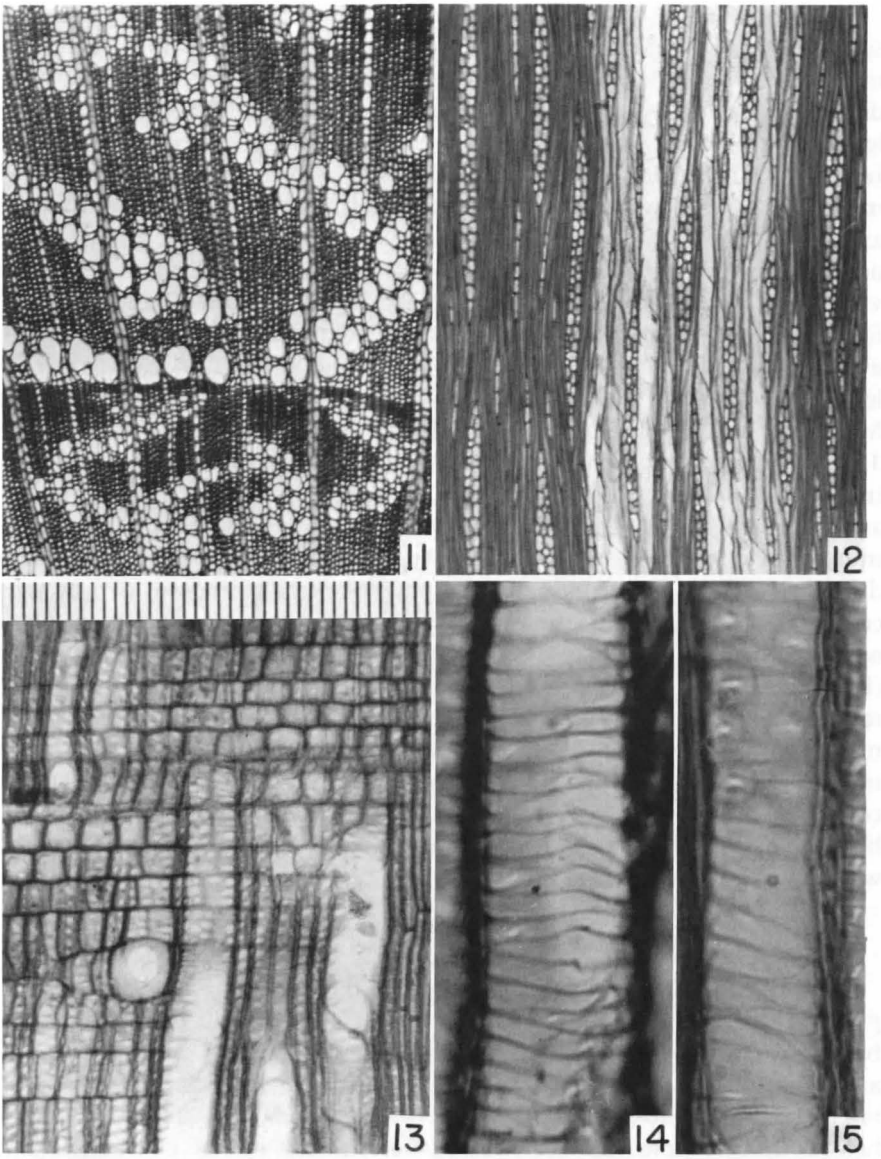

Fig. 11–15. Wood sections of *Chimonanthus praecox* (*Carlquist 1550*).—11. Transection, showing growth ring and large diagonal patterns of vessels.—12. Tangential section; large groups of vessels seen in longisection.—13. Radial section, illustrating ray cell shape and a perforated ray cell.—14. Vessel wall from radial section; bandlike thickenings evident.—15. Vessel wall from radial section; circular pits above. (Fig. 11–12, magnification scale above Fig. 1; Fig. 13, scale above Fig. 13 [divisions = 10 μm]; Fig. 14, scale above Fig. 4.)

Idiospermum australiense (*Hyland 3183*) (Fig. 16–20). Growth rings absent. Vessels solitary or in groups (usually radial chains, Fig. 16). Mean number of vessel per group, 1.67. Perforation plates simple. Mean vessel diameter, 134 μm. Mean vessel wall thickness, 6.9 μm. Mean vessel-element length, 329 μm. Mean number of vessels per mm^2 of transection = 7.2. Intervascular pits polygonal in outline (Fig. 19), probably related to crowding, about 16 μm in diameter, apertures elliptical. Vessel-ray and vessel-axial parenchyma pits alternate, opposite, or scalariform (Fig. 20), apertures nearly as wide as pit cavities. No helical bands or thickenings present in vessels. Tyloses present, common in vessels, thin walled (Fig. 18). Imperforate tracheary elements are all fiber-tracheids; pits sparse, with pit cavities about 2 μm in diameter; pit apertures long and slitlike, exceeding in their length the diameter of the pit cavities. Mean fiber-tracheid length, 539 μm. Mean fiber-tracheid diameter, 27 μm. Mean thickness of fiber-tracheid walls, 4.1 μm. Axial parenchyma both paratracheal and apotracheal; although apotracheal cells are more conspicuous, groupings of axial parenchyma cells around vessels which represent more than chance contacts of diffuse cells must be said to be present (Fig. 16). Apotracheal cells present as diffuse or diffuse-in-aggregates. Axial parenchyma present as strands of two or three cells (Fig. 17). Both uniseriate and multiseriate rays present, these about equally common; by far the majority of the multiseriate rays are biseriate (Fig. 17). Mean height of uniseriate rays, 261 μm. Mean height of multiseriate rays, 386 μm. Ray cells erect, square, and procumbent; procumbent cells more common than square or erect cells (Fig. 18). Erect cells can be found in shorter uniseriate rays and in wings of multiseriate rays (Fig. 17). Ray cells with moderately thick walls. As seen in radial sections, borders may be seen on pits interconnecting ray cells, especially those on the tangential walls. Wood nonstoried.

ECOLOGICAL CONCLUSIONS

The habitats of the three genera studied here are unlike. *Chimonanthus praecox* extends into central and northern China; it occurs on cliffs and banks (Nicely 1965). In these habitats it occurs in full sun; moderate drought and certainly freezing characterize the habitats of *C. praecox*. *Chimonanthus* is a deciduous shrub in which the flowers appear in late winter or early spring before leaves unfold. Both species of *Calycanthus* can be characterized as riparian, although *C. floridus* occurs in moist woodland as well (Nicely 1965; Small 1933). Both species are subject to frost. Both species are deciduous shrubs which flower after leaves unfold. *Idiospermum australiense* grows in perpetually moist soils of rain forest near the Daintree River in northern Queensland (Blake 1972). Frost is unknown in this region at the elevations where *Idiospermum* grows. Unlike the other genera, *Idiospermum* is a tree.

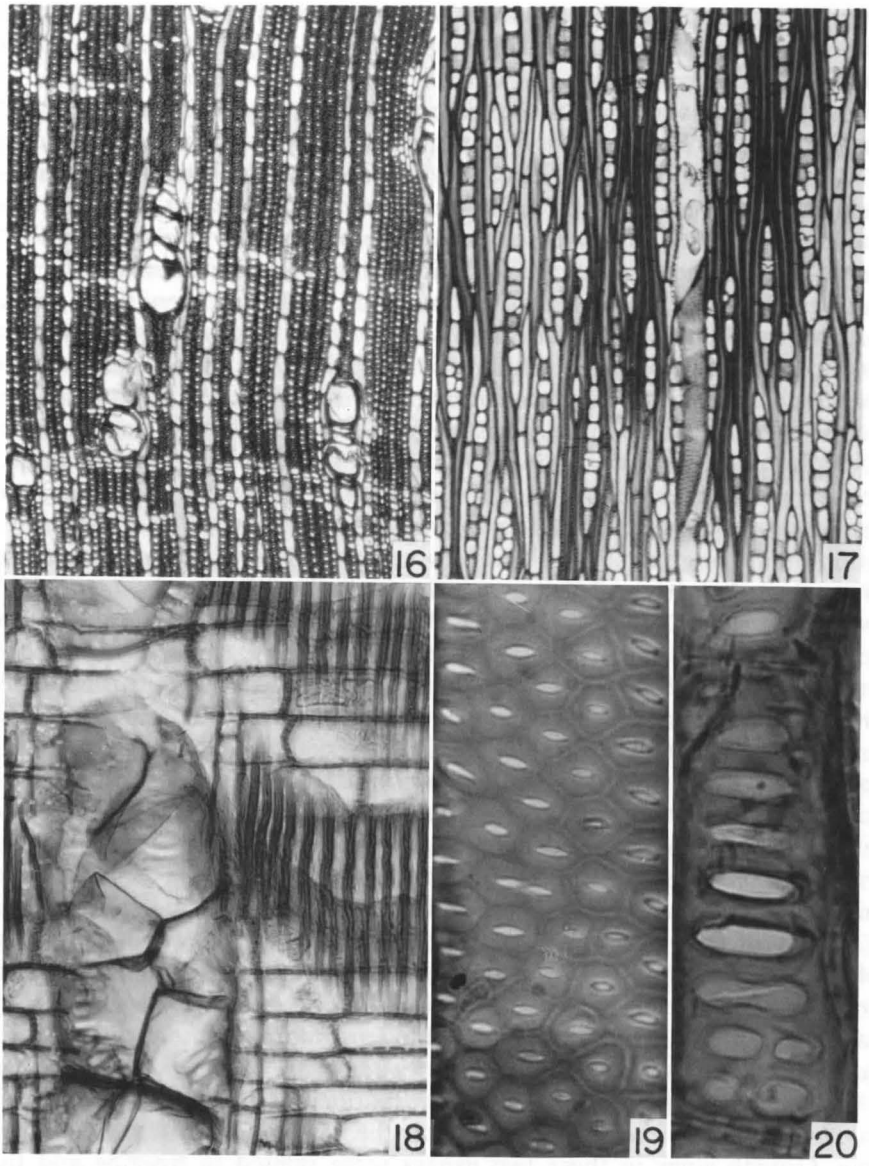

Fig. 16–20. Wood sections of *Idiospermum australiense* (*Hyland 3183*).—16. Transection; transverse aggregations of axial parenchyma visible, and some paratracheal groupings of axial parenchyma cells adjacent to vessels.—17. Tangential section; fiber-tracheids are dark, remainder of axial xylem is parenchyma.—18. Radial section, illustrating a vessel filled with tyloses.—19. Vessel from tangential section showing intervascular pitting.—20. Vessel-ray pitting on vessel wall from radial section. (Fig. 16–17, magnification scale above Fig. 1; Fig. 18, scale above Fig. 13; Fig. 19–20, scale above Fig. 4.)

As an emergent species (also reported in regrowth areas), *Idiospermum* would be expected to have a high rate of transpiration. *Idiospermum* is not deciduous.

These distinctive ecological preferences can be correlated with data from wood anatomy. With respect to water relations, three quantitative features of vessel elements correlate closely with habitat: vessel diameter, vessel-element length, and number of vessels per mm^2 (Carlquist 1966, 1975). Narrower vessels, shorter vessels, and more numerous vessels per mm^2 of transection characterize phylads in drier habitats as contrasted with vessel features of their respective relatives in wetter localities. These three vessel features can be combined into an index termed Mesomorphy (Carlquist 1977): mean vessel diameter (microns) multiplied by mean vessel-element length (microns) divided by mean number of vessels per mm^2. For the species studied here, Mesomorphy values are: *Calycanthus floridus* var. *floridus,* 124; *C. floridus* var. *laevigatus,* 50; *C. occidentalis,* 131; *Chimonanthus praecox,* 90; *Idiospermum australiense,* 6100. The differences among the species of *Calycanthus* and *Chimonanthus* are not great, and no interpretation should be given those differences, especially in view of the provenance of woods from cultivated specimens. However, the difference between those two genera and *Idiospermum* is considerable. Such differences are certainly not unprecedented, and a range in this magnitude may be found, for example, within the genus *Pittosporum* (Carlquist 1981). Such a range can be interpreted ecologically: the moist habitat of *Idiospermum* combined with the sunniness and heat intermittently prevalent there undoubtedly result in transpiration of large volumes of water per unit time, hence the wideness of vessels. *Calycanthus* and *Chimonanthus* have narrower vessels; this may be related to their status as understory (often) or exposed shrubs which would transpire less water than equivalent stems of *Idiospermum.* However, the large number of vessels per mm^2 and the shortness of vessel elements in *Calycanthus* and *Chimonanthus* suggest a xeromorphic wood pattern in which greater safety is achieved. This safety may not be related so much to drought as to frost, although both are likely to be involved. Low Mesomorphy values in *Illicium* are probably related to frost more than to drought (Carlquist 1982).

In this connection, the marked growth rings of *Calycanthus* and *Chimonanthus* are noteworthy. In latewood, the vessels are numerous and narrow. Growth rings in these two genera seem related to freezing and the deciduous habit. The growth rings may be referred to the rather unusual Type VIII in the growth ring classification offered earlier (Carlquist 1980). The absence of growth rings in *Idiospermum* is related to lack of deciduousness and lack of seasonality in the habitat where it occurs. Fiber-tracheids in Calycanthaceae cannot really be considered a cell type which forms a conducting tissue auxiliary to vessels. Pits in fiber-tracheids are too small and few, so that the fiber-tracheids are essentially mechanical cells.

As an emergent species (also reported in regrowth areas), *Idiospermum* would be expected to have a high rate of transpiration. *Idiospermum* is not deciduous.

These distinctive ecological preferences can be correlated with data from wood anatomy. With respect to water relations, three quantitative features of vessel elements correlate closely with habitat: vessel diameter, vessel-element length, and number of vessels per mm^2 (Carlquist 1966, 1975). Narrower vessels, shorter vessels, and more numerous vessels per mm^2 of transection characterize phylads in drier habitats as contrasted with vessel features of their respective relatives in wetter localities. These three vessel features can be combined into an index termed Mesomorphy (Carlquist 1977): mean vessel diameter (microns) multiplied by mean vessel-element length (microns) divided by mean number of vessels per mm^2. For the species studied here, Mesomorphy values are: *Calycanthus floridus* var. *floridus,* 124; *C. floridus* var. *laevigatus,* 50; *C. occidentalis,* 131; *Chimonanthus praecox,* 90; *Idiospermum australiense,* 6100. The differences among the species of *Calycanthus* and *Chimonanthus* are not great, and no interpretation should be given those differences, especially in view of the provenance of woods from cultivated specimens. However, the difference between those two genera and *Idiospermum* is considerable. Such differences are certainly not unprecedented, and a range in this magnitude may be found, for example, within the genus *Pittosporum* (Carlquist 1981). Such a range can be interpreted ecologically: the moist habitat of *Idiospermum* combined with the sunniness and heat intermittently prevalent there undoubtedly result in transpiration of large volumes of water per unit time, hence the wideness of vessels. *Calycanthus* and *Chimonanthus* have narrower vessels; this may be related to their status as understory (often) or exposed shrubs which would transpire less water than equivalent stems of *Idiospermum.* However, the large number of vessels per mm^2 and the shortness of vessel elements in *Calycanthus* and *Chimonanthus* suggest a xeromorphic wood pattern in which greater safety is achieved. This safety may not be related so much to drought as to frost, although both are likely to be involved. Low Mesomorphy values in *Illicium* are probably related to frost more than to drought (Carlquist 1982).

In this connection, the marked growth rings of *Calycanthus* and *Chimonanthus* are noteworthy. In latewood, the vessels are numerous and narrow. Growth rings in these two genera seem related to freezing and the deciduous habit. The growth rings may be referred to the rather unusual Type VIII in the growth ring classification offered earlier (Carlquist 1980). The absence of growth rings in *Idiospermum* is related to lack of deciduousness and lack of seasonality in the habitat where it occurs. Fiber-tracheids in Calycanthaceae cannot really be considered a cell type which forms a conducting tissue auxiliary to vessels. Pits in fiber-tracheids are too small and few, so that the fiber-tracheids are essentially mechanical cells.

The distribution of helical thickenings in vessels of Calycanthaceae is noteworthy. Such helices have been noted in plants subject to pronounced drought (Webber 1936, Carlquist 1966) as well as to frost, as in *Illicium* (Carlquist 1982) where none of the species occurs in areas where drought could be said to occur. Either drought or freezing could result in higher tensions in the water columns of vessels; because of the increase in surface of the helices, enhanced adhesion of water might counter the tendency of air to enter vessels under such conditions (Carlquist 1983). In Calycanthaceae as in Illiciaceae, the most pronounced helices occur in vessels of species which grow in areas subject to more frost (*Chimonanthus praecox*), and complete absence of helices characterizes tropical species (*Idiospermum australiense*). Both species of *Calycanthus* studied have helices in latewood vessels but not in earlywood; this would correlate with the likelihood of physiological drought only for a limited period (perhaps during winter cold). Growth rings in *Chimonanthus* are more pronounced than those of *Calycanthus,* a fact which parallels the occurrence of helices in all vessels of *Chimonanthus* as compared to occurrence only in latewood vessels of *Calycanthus.*

The presence of simple perforation plates exclusively in Calycanthaceae is of interest with respect to ecology. *Idiospermum* has simple perforation plates only, as noted by Wilson (1979); the presence of scalariform plates claimed in Blake's (1972) paper may be a mistake based on scalariform vessel-ray pitting (Fig. 20) in *Idiospermum.* Calycanthaceae have been considered a group with many primitive features, so that presence of specialized perforation plates might at first glance be unexpected. Scalariform perforation plates seem to occur in groups of dicotyledons which have had an unbroken history of occupancy in mesic habitats (Carlquist 1975). If this axiom is true, ancestors of Calycanthaceae have not had an unbroken occupancy of mesic sites, although the family today does have preferences for wet sites. This is not an unusual curriculum for a group, in my opinion. To cite an extreme example, Asteraceae as a group must have begun with simple perforation plates; the family probably occurred in moderately or intermittently mesic environments. From such ancestry, numerous phylads of the family have moved into dry areas—some quite arid—but a few have moved into areas much wetter than those occupied by their ancestors: some are even aquatic plants.

SYSTEMATIC AND PHYLOGENETIC CONCLUSIONS

Calycanthus and *Chimonanthus* are close in terms of wood features. *Chimonanthus* has a greater tendency toward relatively short multiseriate rays (compare Fig. 8 and 12). As mentioned earlier, *Calycanthus* has helical thickenings only in latewood vessels, whereas *Chimonanthus* has helices in all vessels (and has more marked growth rings). Close relationship between

the two genera is indicated by many features, but among the most striking are diagonal bands of vessel aggregations (Fig. 1, 7, 11), the curious distribution of axial parenchyma (vasicentric scanty plus scattered parenchyma, which may be termed diffuse, only at the end or beginning of a growth ring), and even such features as perforated ray cells (mentioned for the family by Chalk and Chattaway 1933).

The two species of *Calycanthus* differ merely in quantitative respects. Differences between the two varieties of *C. floridus* (formerly regarded as two species) are likewise quantitative, as can be seen in terms of ray dimension and ray cell sizes (compare Fig. 2 and 3).

Idiospermum does differ from the pair of genera *Calycanthus* and *Chimonanthus* in a number of respects; these differences have been stressed by Wilson (1979). Wilson cites the larger vessel dimensions of *Idiospermum,* although he wisely does not include these among the reasons why he thinks *Idiospermum* should be segregated in a separate family. The difference in dimensions and in vessel density are, as demonstrated in numerous families of dicotyledons, indicators of difference in ecology and are not indicative of degree of relationship. The same is true of whether growth rings are present (ring porous) or absent (diffuse porous). Such differences (mentioned by Wilson) can be seen in such a close pair of species as *Illicium parviflorum* Michx. and *I. cubense* A. C. Smith (Carlquist 1982), which some authors consider conspecific.

Helices are absent in vessels of *Idiospermum,* as noted by Wilson (1979), but they are also absent in most vessels of *Calycanthus.* Coexistence within a group of species without helices and species which possess them is not unusual; *Illicium* (Carlquist 1982) serves as a convenient example.

Metcalfe and Chalk (1950) alleged that Calycanthaceae have vasicentric tracheids, and Wilson (1979) cited lack of them as a distinction for *Idiospermum.* My studies show presence of vascular tracheids in latewood of *Chimonanthus* (but not in *Calycanthus*). The concept of "vasicentric tracheids" needs revision, and I believe reference of vascular tracheids in *Chimonanthus* to that concept is incorrect.

Thus we are left with only a single supposed distinction of significance, distribution of axial parenchyma. Wilson (1979) claims that in *Idiospermum* axial parenchyma is diffuse and diffuse-in-aggregates. This is true, but also evident is a more than chance association of axial parenchyma with vessels (Fig. 16). Thus, paratracheal parenchyma must be added to the description of *Idiospermum* wood.

At the same time, *Chimonanthus* and *Calycanthus,* which have a form of paratracheal axial parenchyma (vasicentric scanty) were claimed by Metcalfe and Chalk (1950) and Wilson (1979) to lack diffuse parenchyma. However, as noted earlier, the last-formed latewood and the earliest-formed earlywood in this pair of genera does contain diffuse parenchyma. Thus, except for the

seasonality of this parenchyma, all contrast in wood features claimed by Wilson to differentiate *Idiospermum* from the other genera can be said either not to hold or else to be indicative of ecological differences among the genera.

Similarities among the genera, on the other hand, are very persuasive, and include such features as presence of tyloses, predominance of uniseriate and biseriate rays (with erect cells in short uniseriate rays in wings of multiseriate rays, and square to procumbent cells in longer multiseriate rays and in multiseriate portions of multiseriate rays), presence of simple perforation plates, and presence of fiber-tracheids with small sparse pits as the imperforate tracheary element type.

With respect to features of the flower, fruit, and embryo, Wilson (1976) notes differences between *Idiospermum* and the other genera, but these can easily be attributed to adaptations to the distinctive ecology of *Idiospermum,* and are manifold expressions of that habitat. *Idiospermum* has a single carpel (rarely two), a single large seed per fruit, and a seedling with three or four large hypogeal cotyledons. These contrast with numerous carpels per flower, numerous seeds per fruit, and two relatively small epigeal cotyledons in *Calycanthus* and *Chimonanthus.* The seedlings of *Idiospermum* must germinate in shaded locations. Therefore, these seedlings must draw on more massive food reserves, such as the large cotyledons contain, in order to grow to upper, better-illumined levels where photosynthesis can reach the compensation point. With such large cotyledons, elevation of such massive structures above the surface of the soil would be difficult to achieve with anything but a very stout hypocotyl—an uneconomical device. Raising of the cotyledons above the soil surface would be of no selective value because in an understory situation, light would be too dim for the cotyledons to offer appreciable photosynthetic function. Thus the major distinctions *Idiospermum* has with respect to flower, fruit, embryo, and seedling may be attributed, as with distinctions in wood anatomy, to adaptation by an arboreal growth form to a tropical rain forest habitat.

Sterner and Young (1980) stress differences between *Idiospermum* on the one hand and *Calycanthus* and *Chimonanthus* on the other. These differences, however, may well relate to adaptations to types of herbivores where the genera respectively grow. Moreover, Young (personal communication) concedes that *Idiospermum* must be regarded as a sister genus to the other genera, whatever the rank one wishes to accord it.

Wilson (1976, 1979) wisely stresses that in determining whether or not to segregate *Idiospermum* as a separate family, we must assess whether or not it must have had common ancestry with the calycanthoids (*Calycanthus, Chimonanthus,* and presumably *Sinocalycanthus*), or whether *Idiospermum* could have originated independently. Although Wilson (1976, 1979), Sterner and Young (1980) and Cronquist (1981) have recognized Idiospermaceae, Thorne (1976, 1983) and Dahlgren (1980) recognize two subfamilies, Idio-

spermoideae and Calycanthoideae, of Calycanthaceae. The summation of evidence does point to common ancestry of the two groups. To recognize Idiospermaceae as a separate family overstresses the multiple expressions of a single basic difference, the tropical rain forest ecology of *Idiospermum* and the adaptations to that habitat. I endorse Thorne's treatment, consequently. With older relict groups such as one expects within Annonales (Magnoliales, Laurales), one expects more extinction of intermediate genera.

The closest relationships of Calycanthaceae appear to be with Monimiaceae. The wood features of Calycanthaceae can be matched with those of some Monimiaceae, judging from the data of Garratt (1934) and Lemesle and Pichard (1951). Because Monimiaceae is a larger group, more polymorphism in wood anatomy can be expected, and thus a match within this broad range is more likely than within a small or ecologically uniform group. Further detailed studies are needed, because only a portion of Monimiaceae has been investigated with respect to wood. Interestingly, the chromosome number $2n = 22$ has been found in *Idiospermum* (Blake 1972) as well as *Calycanthus* and *Chimonanthus* (Darlington and Janaki Ammal 1945), another strong indication that *Idiospermum* is closely related to the calycanthoids. The chromosome number $n = 22$ has been found in atherospermatoid and hortonioid Monimiaceae as well as in Monimiaceae sensu stricto (Raven 1975), which suggests affinity to Calycanthaceae.

LITERATURE CITED

Blake, S. T. 1972. *Idiospermum* (Idiospermaceae), a new genus and family for *Calycanthus australiensis*. Contrib. Queensland Herb. 12:1–37.

Carlquist, S. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. Aliso 6(2):25–44.

———. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley. 259 p.

———. 1977. Wood anatomy of Onagraceae: additional species and concepts. Ann. Missouri Bot. Gard. 64:627–637.

———. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. Aliso 9:499–553.

———. 1981. Wood anatomy of Pittosporaceae. Allertonia 2:355–392.

———. 1982. Wood anatomy of *Illicium* (Illiciaceae): phylogenetic, ecological, and functional interpretations. Amer. J. Bot. 69:1587–1598.

———. 1983. Wood anatomy of Onagraceae: further species; root anatomy; significance of vestured pits and allied structures in dicotyledons. Ann. Missouri Bot. Gard. 69:755–769.

Chalk, L., and M. M. Chattaway. 1933. Perforated ray cells. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 113:82–92.

Cheng, W.-C, and S.-Y. Chang. 1964. Genus novum calycanthacearum Chinae orientalis. Acta Phytotax. Sinica 9:137–139.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York. 1262 p.

Dahlgren, R. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80:91–124.
Darlington, C. D., and E. K. Janaki Ammal. 1945. Chromosome atlas of cultivated plants. George Allen & Unwin, Ltd., London. 397 p.
Garratt, G. A. 1934. Systematic anatomy of the woods of the Monimiaceae. Trop. Woods 39:18–43.
Kukachka, B. F. 1977. Sectioning refractory woods for anatomical studies. U.S. Forest Serv. Res. Note FPL-0236:1–9.
Lemesle, R., and Y. Pichard. 1954. Les caractères histologiques du bois des Monimiacées. Rev. Gén. Bot. 61:69–95.
Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 p.
Nicely, K. A. 1965. A monographic study of the Calycanthaceae. Castanea 30:38–81.
Raven, P. R. 1975. The bases of angiosperm phylogeny: cytology. Ann. Missouri Bot. Gard. 62:724–764.
Small, J. K. 1933. Manual of the southeastern flora. Privately published, New York. 1554 p.
Stern, W. L., and S. Greene. 1958. Some aspects of variation in wood. Trop. Woods 108: 65–71.
Sterner, R. W., and D. A. Young. 1980. Flavonoid chemistry and the phylogenetic relationships of the Idiospermaceae. Syst. Bot. 5:432–437.
Thorne, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6(4):57–66.
———. 1976. A phylogenetic classification of the Angiospermae. Evol. Biol. 9:35–106.
———. 1983. Proposed new realignments in the angiosperms. Nord. J. Bot. 3:85–117.
Webber, I. E. 1936. The woods of sclerophyllous and desert shrubs and desert plants of California. Amer. J. Bot. 23:181–188.
Wilson, C. L. 1976. Floral anatomy of *Idiospermum australiense* (Idiospermaceae). Amer. J. Bot. 63:987–996.
———. 1979. *Idiospermum australiense* (Idiospermaceae)—aspects of vegetative anatomy. Amer. J. Bot. 66:280–289.

Claremont Graduate School, Pomona College, and Rancho Santa Ana Botanic Garden, Claremont, California 91711.

Footnote

The writer is grateful to B. P. M. Hyland of the C.S.I.R.O. Division of Forest Research, Atherton, Queensland, for a wood sample of *Idiospermum.*